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Research Article

Preservation biases in the fossil record distort species ecological niche and distribution models

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Ecological niche models (ENMs) increasingly leverage the fossil record to understand species' environmental associations and predict their geographic distributions. However, fossils do not occur uniformly through time and space, which can compromise the robustness of ENMs and thus affect ecological conclusions. Here, we assessed how preservation biases in the fossil record impact our ability to reconstruct ecological niches and distributions of North American small mammals during the late Quaternary. First, using small mammal fossil occurrences and associated depositional environment data, we quantified preservation potential (the likelihood that a given environment supports fossil preservation) and the preservation niche (environmental correlates of preservation) for three late Quaternary time periods (the Last Glacial Maximum, the deglacial period, and the Holocene). Second, we imposed the calculated preservation potential on simulated distributions of six virtual species to evaluate its impact on reconstructing species niches and geographic distributions through time. We found that preservation potential was highest in the Holocene and lowest during the deglacial period, with the differences driven by variations in climate and the prevalence of Holocene archaeological sites. In all intervals, warm, wet, and highly seasonal environments exhibited low preservation potential. These spatial and temporal differences in preservation potential significantly influenced niche reconstructions and geographic predictions, particularly impeding model quality when species niches extended beyond the preservation niche. We warn that such distortions can lead to erroneous ecological inferences, including inaccurate predictions of species responses to environmental changes and mischaracterizations of community assembly processes. We propose that our approach to modelling preservation potential can be applied across different regions, time periods, and taxonomic groups to help correct distortions caused by sampling biases through weighted background point selection that reflects these processes. Ultimately, this framework enhances the ability to disentangle true ecological patterns from preservation artifacts, improving the reliability of fossil-based ecological and evolutionary inferences.

Keywords: ecological niche model, fossil, preservation, sampling bias, species distribution model, taphonomy



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Introduction

Characterizing species' abiotic niches (a.k.a. Grinnellian niche; Grinnell 1917) is fundamental for predicting their distributions and responses to environmental change, and for understanding how ecological communities form. However, many species' present-day realized niches have been truncated by human activities and reflect only a subset of environmental conditions they can tolerate, limiting our understanding of abiotic tolerances and the transferability of inferred niches in space and time (Raiter and Hawlena 2024, Bellvé et al. 2025a). This limitation has prompted a growing call over the last two decades to 'put the dead to work' (Dietl and Flessa 2011, p. 30); that is, to use paleo-records (e.g. fossils) to better understand species' vulnerabilities and their responses to environmental change, as well as the ecological drivers of declines and extinctions (Willis and Birks 2006, Dietl and Flessa 2011, Maguire et al. 2015, Lima-Ribeiro et al. 2017, Fordham et al. 2020, Faurby et al. 2024). Fossils are also critical for reconstructing the niches of extinct animals, offering unique insights that cannot be obtained from modern data alone. In particular, the fossil record can offer great utility for ecological niche models (ENMs), as it can provide insights into species distributions prior to, or during, periods of environmental change (Nogués-Bravo et al. 2008, Svenning et al. 2011, Varela et al. 2011, Moreno-Amat et al. 2017, Faurby and Araújo 2018, Bellvé et al. 2025, Blois et al. 2025), and even improve forecasts of distributions under future climates (Lima-Ribeiro et al. 2017). ENMs combine species occurrences with associated environmental information to quantify a species' abiotic niche and predict its geographic distribution (Elith et al. 2010), but they assume that occurrence records accurately reflect the environments occupied by a species, or that any spatial or environmental biases in those records have been adequately corrected for (Phillips et al. 2009). Without such correction, however, ENMs can, for example, misinterpret regions with low sampling effort as areas of low habitat suitability (Kramer-Schadt et al. 2013). Just as present-day occurrence records are subject to a number of biases – such as uneven sampling effort, anthropogenic absences, etc. (Syfert et al. 2013, Lima-Ribeiro et al. 2017, Raiter and Hawlena 2024) – the fossil record carries its own unique spatial and environmental biases (Bellvé et al. 2025), since fossil formation or preservation are inherently uneven across space and time (Signor and Lipps 1982, Behrensmeyer et al. 2000, Noto 2011). Although considerable progress has been made in mitigating biases in contemporary ENMs (Syfert et al. 2013, Qiao et al. 2017, Botella et al. 2020, Baker et al. 2022), correcting for biases in fossil-based ENMs remains relatively underexplored (Blois et al. 2025; although see Block et al. 2016, Inman et al. 2018, Bellvé et al. 2025). As such, understanding and quantifying spatiotemporal biases in fossil preservation will be crucial in accurately reconstructing species' past niches and distributions.

Preservation biases (Box 1) vary across spatial scales and change through time. For example, in terrestrial

environments, microclimates conducive to fossil preservation are commonly found in caves or beneath outcrops, where remains are shielded from rain and weathering (Behrensmeyer 1978, Castillo et al. 2001). While the microclimatic conditions that facilitate fossilization are relatively well-understood (Noto 2011, Pokines and Spiegel 2021), preservation potential (Box 1) at broader, continental scales remains poorly resolved, potentially impacting ENMs in particular, which are commonly created at regional to continental scales, particularly for past distributions (Blois et al. 2025). An initial investigation of the climatic associations of articulated avian fossils over the last ~ 161 million years suggested that warm-humid environments may favor preservation over cool-dry climates (Gardner et al. 2016). In contrast, humid and/or strongly temperature-seasonal regions accelerated DNA fragmentation in late Pleistocene mammals (Kistler et al. 2017), consistent with experimental results on the microclimatic drivers of bone weathering (Behrensmeyer 1978, Pokines et al. 2016). Similarly, our understanding of how preservation biases vary through time remains limited. Generally, remains from deeper time periods are less abundant due to increased opportunities for fossils to be destroyed or further buried (Behrensmeyer 1978, Behrensmeyer and Hill 1988, Noto 2011; although see Gardner et al. 2016). However, shifts in climate, changes in prevalence of different depositional environments (Box 1), or discrete events such as volcanic eruptions (Fritz 1986, Maguire et al. 2016, Lafuente Diaz et al. 2018) can affect the temporal pattern of fossil preservation. Finally, preservation varies among taxa, with larger species, species with hard elements, or those inhabiting environments conducive to preservation (e.g. soft sediments, caves, etc.) better represented in the fossil record (Signor and Lipps 1982, Behrensmeyer et al. 2000). Efforts to correct these biases have shown promise. For example, Block et al. (2016) improved the predictive accuracy of species distributions by creating individual climate, preservation, and discovery models, and then averaging their ranking for each spatial grid cell. Similarly, Inman et al. (2018) improved the performance of hindcasted distribution models for plant species by correcting spatial sampling biases in North American packrat (*Neotoma* spp.) middens by weighting the selection of background points to mimic the sampling biases in their presence records (i.e. the 'FactorBiasOut' method; Phillips et al. 2009). Despite these efforts, gaps remain in understanding how specific environmental conditions and time periods influence preservation potential and, thus, our ability to reconstruct species' ecological niches and distributions.

Here, we aim to quantify preservation bias in the late Quaternary fossil record and assess how spatiotemporal variation in preservation impacts reconstructions of ecological niches and distributions of simulated North American small mammals during this period. We adopt a three-tiered framework (Fig. 1). First, we use dated small mammal fossil localities to quantify the 'preservation niche' and map 'preservation potential' (Box 1) for small mammal fossils generally

Box 1. Glossary of terms commonly used in our manuscript.

Depositional environment – The physical or biological setting in which fossils accumulate and are eventually buried and preserved in the geologic record. This study uses the NeotomaDB classifier for depositional environment which refers to the present-day depositional environment of the locality.

Preservation bias – The non-random influence of environmental factors on fossil formation and preservation across space and time. Here, we use this as a collective term to describe the ‘preservation niche’ and the landscape of ‘preservation potential’ we create with principal component analyses (PCAs) and maximum entropy algorithm (MaxEnt) models, respectively, and how these impact our ability to create ENMs.

Preservation potential – The likelihood (ranging from 0 to 1) that a given environment is suitable for fossil preservation, with higher values indicating a greater probability of fossil occurrence. In this study, preservation potential refers to the predictive geographic raster layers generated using MaxEnt, which represent modeled probabilities of fossil presence across the landscape.

Preservation niche – The range of environmental conditions under which fossil preservation is most likely to occur. In our study, the preservation niche is captured by PCA models based on small mammal fossil occurrences and associated depositional environments.

Background environment – The set of environmental conditions sampled from the broader landscape and used to calibrate models of fossil preservation. In our study, the background environment was represented by 99 999 randomly sampled points from the environmental layers for each time period.

Sample model – Ecological niche models (ENMs) constructed using data drawn from either the unbiased abundance layer or the biased abundance layer for a given species and time period.

Unbiased sample – Occurrence samples drawn from the unbiased abundance layer representing the ‘true’ distribution of a given species during a specific time period.

Biased sample – Occurrence samples drawn from the biased abundance layer representing the ‘true’ distribution modified by preservation potential of a given species during a specific time period.

Niche reconstruction accuracy – A measure of how closely the sample PCA results align with the reference niche constructed from the 5000-point ‘true’ PCA.

Distribution prediction accuracy – A measure of how closely the predictions from sample MaxEnt models match those from the ‘true’ MaxEnt models.

in three time periods: the Last Glacial Maximum (LGM), to capture the cold glacial earth system state; the Holocene period (HOL), to capture the warm interglacial earth system state, and a deglacial period (DG) that represents the transition between the two. Second, for each of the three time periods, we simulate ‘true’ distributions of six virtual species based on the abiotic requirements and ecologies of six extant real-world small mammal species (Supporting information). These simulated ‘true’ species distributions serve as proxies of past distributions, for which perfect knowledge is not available. Third, we apply the preservation potential layers to degrade the simulated true virtual species distributions (Fig. 1A), which we then sample following a ‘virtual ecologist’ approach (Zurell et al. 2010) to evaluate how preservation potential impacts ENM prediction accuracy and our ability to reconstruct a species niche from fossils (Fig. 1B). We additionally investigate the effects of sample size and time period in concert with preservation potential. We predict that 1) preservation potential will distort niche centroids and increase prediction error, 2) these effects will become more pronounced with age, 3) larger sample sizes will mitigate these biases, and 4) species-specific ecological traits will mediate these interactions. Our study is among the first to unite discussions of fossil record biases with their explicit incorporation into ecological niche models, directly demonstrating how fossil preservation biases affect the reconstruction of both species’ niches and distributions. Our framework offers a pathway for other researchers to test these effects across different systems and time periods.

Material and methods

Environmental data

We used six environmental layers as predictors for both preservation potential (section ‘Preservation potential and the preservation niche’) and reconstructing virtual species niches (section ‘Preservation niche’) in the late Quaternary (Supporting information): elevation, terrain slope, mean annual temperature, temperature seasonality, annual precipitation, and precipitation seasonality. These variables cover aspects of physical and climatic environments that are relevant to both the formation of fossils (Behrensmeyer 1978, Behrensmeyer and Hill 1988, Behrensmeyer et al. 2000, Noto 2011) and the environmental niches of small mammals (Beaumont et al. 2016) across our study area of North America (Supporting information).

All layers had a 1 × 1 km resolution and were sourced from CHLSA-TraCE21K (Karger et al. 2023), with the exception of slope, which was derived from the CHLSA-TraCE21K digital elevation model based on the surrounding eight grid cells. We used the NaturalEarth ‘North American historic lakes’ shapefile (ver. 5.0.0; naturalearthdata.com) to mask out all major natural water bodies for the present, and also the Holocene assuming that the water bodies did not substantially change over the last 6,000 years. For the LGM and DG, we additionally masked out pluvial waterbodies, which were a defining landscape feature during these two time periods (ver. 4.0.0; naturalearthdata.com). Glaciers were masked using the respective glacier elevation layer for each

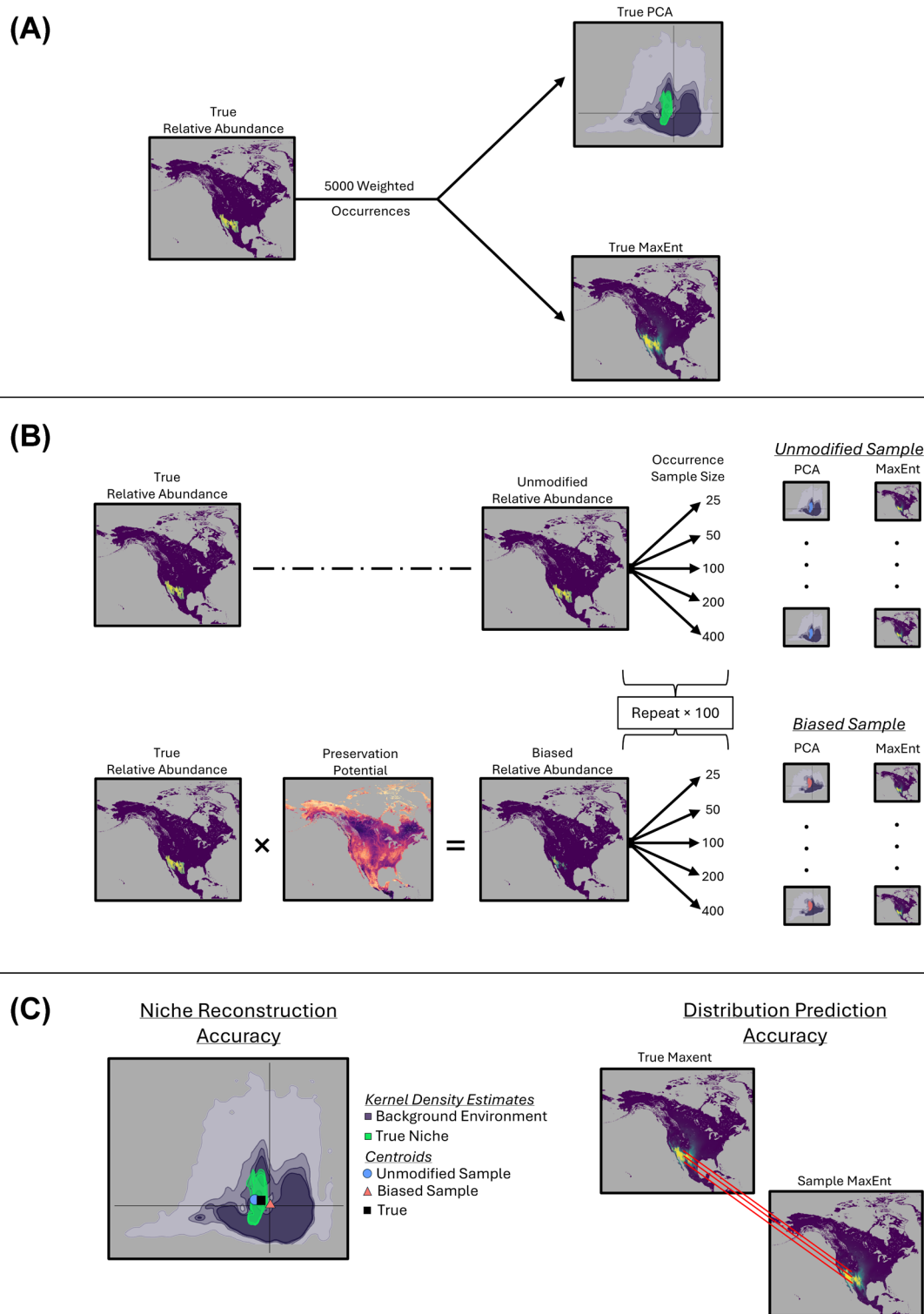


Figure 1. Conceptual workflow for the virtual ecology sampling regimes for each species and time period. We first sampled the 'true relative abundance' layer to create the true principal component analysis (PCA) and maximum entropy (MaxEnt) models for evaluation (A). We then created the 'unbiased' and 'biased relative abundance' layers, which we sampled 100 times using the weighted occurrences. These samples were then used to fit the PCA and MaxEnt models (B). Finally, we evaluated the predictive accuracy of PCA and MaxEnt models created from sampling layers to True models based on a sample of pairwise cells (C). The creation of the 'true relative abundance' layer in (A) is outlined in the Supporting information.

time period from the CHELSA-TraCE21K layer set. See the Supporting information for further details.

Preservation potential and the preservation niche

Fossil occurrence data

We used small mammal fossil locality data from the Neotoma Paleocology Database (hereafter NeotomaDB; Williams et al. 2018). Using the 'neotoma2' package (ver. 1.0.2; Vidaña and Goring 2023), we first searched for all vertebrate fossil localities (i.e. collection units in NeotomaDB) within a polygon defining North America, with a maximum age < 35 000 years, to capture all potentially relevant localities. We then filtered these localities to include only those with at least one chronology and at least one small mammal specimen (i.e. any fossil material assigned to Eulipotyphla/Insectivora, Lagomorpha, or Rodentia). Each locality is associated with a depositional environment and preservation processes may differ among these environments (Behrensmeier and Kidwell 1985, Noto 2011). In NeotomaDB, 'depositional environment' refers to the present-day environment associated with a fossil locality (e.g. cave, bog, etc.) and serves as a proxy for conditions under which fossils were preserved. We excluded localities with missing or unknown depositional environments and collapsed the remaining depositional environment types into six broader classes following the hierarchical structure of the 'depositional environment' variable in NeotomaDB, to ensure a sufficient sample size within each category (Supporting information). Because depositional environments represent distinct preservation regimes and do not overlap, we modeled preservation potential separately for each depositional environment. We estimated the overall age range of each locality by converting the chronology age boundaries for the locality to calibrated radiocarbon years before present (ybp) based on the IntCal20 radiocarbon calibration curve (used to convert Northern Hemisphere raw radiocarbon [^{14}C] ages into calendar years for the last 55 000 years; Reimer et al. 2020), dropping any locality that had at least one undefined age boundary or was duplicated. Finally, we excluded localities with a minimum age older than 30 000 ybp. We note that, by treating fossil deposits as individual occurrences, rather than individual specimens, our analysis ignores the potential effects of species abundance on the likelihood of preservation. Inherently, preservation potential would likely be better modelled as a count process, or even a two-stage model (i.e. zero-inflated/hurdle process), with some habitats being more favorable for preservation than others and accumulating greater numbers of specimens. Unfortunately, count data required for such modeling are not presently available in sufficient quality or consistency. For instance, many studies report 'minimum number of individuals' or 'number of identified specimens' for deposits, but these values are not always comparable across datasets, limiting their utility. Alternatively, species richness might be used as a proxy for abundance, as the two are often positively correlated, but the slope of this relationship varies across habitats and along latitudinal gradients (Brodie and Mannion 2023,

Tenorio et al. 2023), precluding a straightforward substitution at the landscape scale. Our treatment of deposits as individual occurrences mitigates these effects to some degree, particularly as we spatially thinned these occurrences to account for spatial autocorrelation among sites (section 'Preservation potential'). See the Supporting information for specific details on our searches for fossil localities, including additional details on depositional environments and locality chronologies.

We examined taphonomy effects separately for different climate regimes by considering three broad time intervals (LGM, DG, HOL), with overlapping buffers added to the interval boundaries to smooth out the edge effects (Foote 2001). To capture the broadest range of possible occurrences given temporal uncertainty in fossil dating, we expanded each time interval beyond its core time period (Supporting information). The LGM interval (30 000–15 000 ybp) contains the North American period of maximum glacial extent. The DG (16 000–11 000 ybp) captures an interval of variable climate including the Bølling-Allerød warming event and the Younger Dryas. The HOL (12 000–500 ybp) covers the pre-industrial warm interglacial climate interval. Localities were assigned to one or more time intervals based on whether the locality age range overlapped with each interval. Ultimately, the final fossil locality dataset comprised 2556 localities across North America, spanning six depositional environments and three time periods from 30 000 to 500 ybp (Supporting information).

Preservation potential

In addition to environmental biases, the fossil record is subject to several reporting biases that can lead to mischaracterizations of the environmental drivers on preservation potential. We identified three distinct reporting biases. First, there is strong autocorrelation among fossil sites, partly arising from the variable precision with which fossil sites are reported (e.g. some studies report coarse spatial resolution to prevent specific site location disclosure, while other locality coordinates are reported precisely). To limit the effect of spatial autocorrelation among fossil sites (Aiello-Lammens et al. 2015) and prevent particular environments from being overrepresented, we spatially thinned fossil localities (hereafter 'occurrences') to 5 km for each time period. A 5 km threshold was chosen as it was a sufficient distance to represent spatially distinct sites, while retaining enough occurrences to create reliable models (Supporting information). Second, the vast majority of small mammal fossil occurrences in NeotomaDB fall within the contiguous USA, largely as a historical artefact of reliance on USA-based vertebrate research efforts during initial creation of the NeotomaDB rather than environmental favourability. To reduce the effect of geopolitical differences, we matched the number of background points selected from each country (Canada, Mexico, and the USA) to the number of fossil occurrences in that country, for each time period. In effect, this allowed us to match the geopolitical sampling biases in the NeotomaDB, and create a more proportionate

representation of each country's environmental space. Third, fossil sites are more likely to be discovered near human habitation due to their general accessibility or exposure during earthworks (a.k.a. 'discovery biases'; Block et al. 2016). We drew a weighted sample of background points within each country, by weighting the probability of cell selection by the distance from the nearest road (Block et al. 2016, Inman et al. 2018), following the 'FactorBiasOut' method (Phillips et al. 2009), to account for the aforementioned discovery bias sampling (Barber et al. 2022). Cells with a presence were excluded from the weighted draw for background points, to avoid over-sampling these environments. Background points were drawn at an equal prevalence as presence points (Barker and MacIsaac 2022, Tong et al. 2023, Rausell-Moreno et al. 2025). See the Supporting information for more details.

We extracted environmental values for fossil occurrences separately for each time period $\times$ depositional environment combination to allow for multimodal environmental response (i.e. different types of fossilization). For each dataset, we trained a MaxEnt model using five-fold cross-validation (CV). As five-fold CV requires a minimum of ~ 14 occurrences per fold, we excluded models with fewer than 70 occurrences to ensure reliable predictions. This threshold also allowed us to retain at least 60 occurrences in each CV replicate training set (10 per predictor across six predictors; Guisan et al. 2017). For each CV model replicate, we generated predictions of preservation potential (i.e. the probability of suitable habitat for small mammal fossil preservation), and summarized the prediction surfaces for each time period and depositional environment by averaging the predictions across replicates. For each time period, we then combined all depositional environment models by taking the maximum probability of each cell, as this best represents the likelihood of fossil occurrence in a given area. Following modelling, we found that the Riverine and Stillwater deposits consistently yielded unreliable predictions of fossil formation due to a lack of environmental correlates specific to these settings and were thus excluded from our predictions of preservation potential. The final suite of preservation potential models included a Holocene-age model of Archaeological depositional environments, and models of Biological and Terrestrial depositional environments for all three time periods (Supporting information). The final output was a small mammal fossil preservation potential layer for each time period, representing the likelihood of the environment in a given location during that time period supporting the fossilization of small mammal remains.

Preservation niche

While the models of preservation potential provide geographic predictions of the suitability of fossil occurrence for each time period, they provide limited insight into the environmental niche of preservation (hereafter preservation niche; Box 1). To examine the preservation niche in n-dimensional environmental space, we used covariance-based principal component analysis (PCA) on centered and scaled environmental

data. This allowed us to visualize the distribution of fossil occurrences relative to the environment of each time period. To do so, we randomly sampled 99 999 points from North America's environmental layers for each time period to calibrate a scaled and centered PCA (Thioulouse et al. 2018). Fossil occurrences were then projected into that PC space, and we created 70, 80 and 90% kernel density estimates (KDEs) around these occurrences to visualize the extent of preservation niche within environmental space.

Virtual species creation

Our overarching goal was to understand how preservation biases affect the reconstruction of species' ecological niches and distributions. However, all paleo-occurrence data are inherently subject to the very biases we sought to evaluate. To circumvent this limitation we developed virtual species, which we modeled after the environmental niches of real-world taxa to ensure ecological realism. To do so, we used a two-step process, first creating ENMs for real contemporary small mammal species, and then abstracting the ENMs to generate virtual species. While these models inevitably contain some spatial biases (Inman et al. 2021), the goal was not to produce perfect distributions or habitat associations but rather to create ecologically realistic virtual species with niches approximating those of real species.

To create virtual species distributions, we first selected six real small mammal species (Supporting information) from the Global Biodiversity Information Facility (GBIF) database, chosen based on the availability of modern occurrence data, their environmental niches, and current distributions in North America. While the GBIF database is known to have sampling biases, our aim was not to create perfect models of these species distributions, but rather to construct ecologically plausible virtual analogs. The selected species included two Rodentia *Microtus pennsylvanicus*, *Neotoma albigula*, two Lagomorpha *Lepus californicus*, *Sylvilagus floridanus*, and two Eulipotyphla *Blarina brevicauda*, *B. carolinensis*, ensuring representation of diverse ecological habits and comprehensive coverage across North America (Supporting information) and present-day environments (Supporting information). Occurrence data for each species was used to train MaxEnt models, which were fitted using a five-fold CV (Supporting information). Models were evaluated using the area under the receiver-operator curve (AUC), which ranges between 0.5 (performing no better than chance) and 1 (perfect prediction; Fielding and Bell 1997) and combines measures of sensitivity and specificity. Variable importance was calculated using jackknife CV within each of the models' five-fold CV replicates (Supporting information). The prefix 'V_' was added to each species name to denote the virtual counterparts; e.g. *M. pennsylvanicus* produces *V_M. pennsylvanicus*.

We used the response curves generated from these real species ENMs to create virtual representations of their niches ('virtualspecies' ver. 1.5.1; Leroy et al. 2016). By deriving statistical moments from these response curves, we parameterized mathematical functions to approximate virtual species'

responses to all environmental variables. These functions were then used to create probability of occurrence surfaces for each virtual species $\times$ time period combination. To assess the performance of these mathematical abstractions, we visually compared the resulting virtual species distributions with the original real species distributions to ensure that they were similar.

Because the probability of fossilization is determined not only by the environment and a species' probability of occurrence but also by a species' abundance (Behrensmeier et al. 2000), we created abundance maps for each virtual species and time period. To do so, we first retained only cell values with probability of occurrence > 0.5 , and then linearly scaled the remaining occurrence probabilities using empirical estimates of the minimum and mean densities of the corresponding real species sourced from empirical studies (Supporting information). We converted these scaled probabilities to relative abundance by dividing each cell by the empirical mean abundance estimate. The final output of this process was 'true' relative abundance layers (Supporting information) for each virtual species $\times$ time period combination, that captured species' core habitat and species-specific abundances in favorable versus unfavorable habitat. While this method lacks the statistical rigor of traditional population models (e.g. N-mixture models) that capture uncertainty in abundance estimates, and is not appropriate for real-world populations, our goal was to capture rough approximations of virtual species abundance to represent its influence on fossilization likelihood. For more details see the Supporting information.

The effect of preservation potential on reconstructing species' niche and distribution

'True' virtual species niche and distribution

We first characterized each virtual species' 'true' niche by drawing 5000 unique presences from the true relative abundance layers, which served as a baseline for comparing sampled models (section "Sample' virtual species niche and distribution"). The environmental values for these presences were extracted and used for two modelling exercises (Fig. 1A). First, the environmental values were centered, scaled, and fitted with a covariance-based PCA to model each virtual species' true environmental niche in multivariate space (hereafter 'true PCA'). Second, we used the same 5000 presences and sampled an additional 5000 background points (Barker and MacIsaac 2022, Tong et al. 2023, Rausell-Moreno et al. 2025) randomly from across North America, excluding sites that already had a presence sample. We then used the environmental data for these locations to train 'true MaxEnt' ENMs for each time period, resulting in 'true' virtual species distributions (Fig. 1A).

'Sample' virtual species niche and distribution

To isolate the effect of preservation potential on niches and distributions, we sampled from two types of layers for each virtual species $\times$ time period combination. First, we sampled from the true relative abundance layer (section 'Virtual species

creation *Virtual species creation*') – this 'unbiased' sample layer provided a control against which to compare the effects of a biased sample (Fig. 1B). Second, we sampled from a 'biased' relative abundance layer, which was created by multiplying the true relative abundance layer by the preservation potential layer (section 'Preservation potential') for the respective time period.

It is well-documented that sample size plays an important role in ENM performance (Wisz et al. 2008). Given the sparsity of the fossil record for many small mammal species, we tested the effect of sample size on model performance and its interaction with virtual species, time period, and preservation biases. Ultimately, we followed a full factorial design (Fig. 1B), using every combination of sample layer type (unbiased or biased), time period, virtual species, and sample size ($n = 25, 50, 100, 200, 400$). All presences were sampled from their respective layers with a weighting based on the cell value (i.e. relative abundance), with an equivalent number of randomly drawn background points. Following the procedure detailed in sections 'Preservation potential' and 'Preservation niche', we then created PCA and MaxEnt sample models for each combination, which we replicated 100 times to capture variability in the sampling process.

Niche reconstruction accuracy

To evaluate our ability to reconstruct a virtual species' true niche, we compared the centroids of the unbiased and biased sample PCA models to those of true PCA. First, we scaled and centered the 5000 true environmental values to calibrate the PCA space for each virtual species $\times$ time period. We then calculated the position of the sampled occurrences for each of the 100 replicates of each virtual species, time period, sample layer, and sample size combination, and then derived their centroids. For each combination, we then derived the centroid of all the replicate centroids and calculated its distance from the respective true centroid as a measure of niche reconstruction accuracy.

Distribution prediction accuracy

To assess the effects of preservation potential on a model's ability to predict a virtual species distribution, we used the occurrence probability layer for each virtual species and time period that resulted from the sample MaxEnt models (biased or unbiased) described in section "Sample' virtual species niche and distribution". Given that our sample regime included 18 000 individual MaxEnt models, generating individual occurrence probability maps was computationally inefficient. Instead, we randomly sampled 100 cells per probability value (i.e. 0–1 at 0.01 increments) from the true virtual species distribution models and extracted their environmental values. This sub-sample captured the full range of habitat suitability values. Using the sample MaxEnt models (both unbiased and biased), we predicted occurrence probabilities for these cells and calculated difference from the true virtual species distributions predicted probability. Prediction errors were then summarized across all sampled cells as the median absolute error (MAE) for each replicate.

Implementation

All data manipulation and analyses were performed in R (ver. 4.5.0; www.r-project.org) using an RStudio interface (ver. 2025.05.1 Build 513 'Mariposa Orchid'). See the Supporting information for more details.

Results

Preservation potential and the preservation niche

The PCA of background environmental variation across North America for the three time periods, based on 99 999 randomly sampled points, revealed that the first two principal components captured approximately 38–39% (PC1) and 25–27% (PC2) of the total variance, respectively (Supporting information). Correlations of PCs with the original environmental variables remained consistent across time periods (Fig. 2A, Supporting information), with PC1 strongly associated with mean annual temperature, annual precipitation, and temperature seasonality, while PC2 was associated with elevation, slope, and precipitation seasonality. The high

percentage of variation explained by the first two axes in all our PCAs indicates that environmental variation in North America is well represented by the first two PCs, and that our three time periods are broadly comparable. Small mammal fossil occurrences were non-randomly distributed within this environmental space (Fig. 2A). Specifically, environments with high mean annual temperatures and annual precipitation were under-represented among small mammal fossil sites, with 70–90% kernel density estimates (KDEs) only partially overlapping those of the background environment sample. This structure was most pronounced in the DG, followed by the LGM and HOL, when the preservation niche was most closely aligned with the prevailing environmental conditions. In the DG and HOL, fossil observations were also sparse in areas with strong temperature seasonality relative to each period's environmental conditions. Predictions from MaxEnt models of preservation potential supported these PCA-based patterns. In all but one model, mean annual temperature and temperature seasonality ranked among the top three predictors (Table 1). All individual models demonstrated strong predictive performance (AUC between 0.69

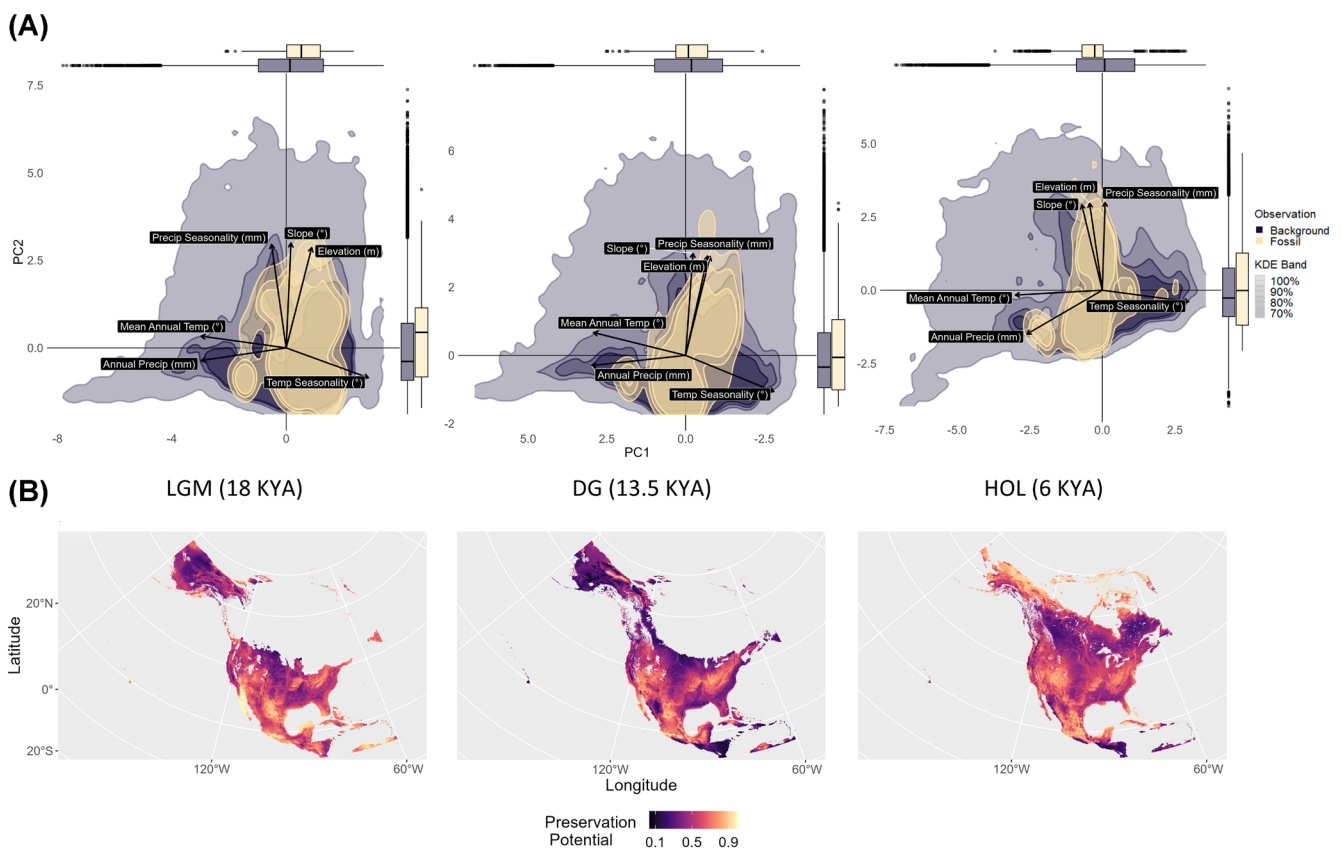


Figure 2. (A) The preservation niche is mapped using the first two principal component (PC) axes, with kernel density estimates (KDE) ranging from 70–100% for the background environment sample (purple), and 70–90% for the fossil occurrences (yellow). Black arrows show environmental vectors of the original variables used to create the principal components. (B) Preservation potential (i.e. probability of a suitable environment for fossil preservation) across North America during the Late Quaternary, shown for the midpoints of the Last Glacial Maximum (LGM), deglacial (DG), and Holocene (HOL) periods. Glaciers and contemporary waterbodies are masked out. Heatmaps, displayed in a Conus Albers projection (EPSG: 5070), use lighter colors to indicate more favorable environments for small mammal fossil preservation.

Table 1. Performance metric and variable contribution of the models for each depositional environment (Supporting information) and time period. Area under the receiver operator curve (AUC) and variable contributions were estimated using five-fold cross-validation. Values shown below time periods indicate the time range (in years before present, ybp, where present is ~ 1950 AD) covered by fossil occurrences.

Time period	Depositional environment	AUC $\pm$ SD	Top predictors (% variable contribution)		
			No. 1	No. 2	No. 3
Holocene (11 700–present)	Archaeological	0.691 $\pm$ 0.009	Mean annual temperature (63.8)	Elevation (13.3)	Temperature seasonality (11.4)
	Biological	0.759 $\pm$ 0.034	Annual precipitation (40.9)	Mean annual temperature (38.2)	Elevation (7.9)
	Terrestrial	0.712 $\pm$ 0.012	Mean annual temperature (57.1)	Temperature seasonality (27.9)	Slope (5.5)
Deglacial (15 000–11 700)	Biological	0.749 $\pm$ 0.055	Mean annual temperature (33.1)	Slope (28.4)	Temperature seasonality (21.5)
	Terrestrial	0.703 $\pm$ 0.025	Mean annual temperature (49.7)	Elevation (22.8)	Temperature seasonality (13.8)
Last Glacial Maximum (21 000–15 000)	Biological	0.740 $\pm$ 0.054	Slope (68.1)	Temperature seasonality (13.2)	Mean annual temperature (7.7)
	Terrestrial	0.686 $\pm$ 0.013	Elevation (26.9)	Temperature seasonality (24.1)	Slope (21.1)

and 0.76; Table 1; Fielding and Bell 1997), indicating that preservation potential was reliably estimated and that differences in sample size among the three time periods had no discernible effect.

Preservation potential of small mammal fossils was lowest during the DG, with 36% of the area having a probability of a suitable environment for preservation $\geq$ 0.50, and a mean probability of 0.45 across North America. In contrast, the LGM and HOL had higher preservation potential, with 57 and 61% of cells, respectively, having a probability of a suitable environment $\geq$ 0.50, and mean probabilities of 0.54 and 0.58, respectively. Preservation potential was geographically consistent across the time periods (Fig. 2B), with high preservation potential in the mountains and deserts of the west and southwest and along the Appalachian mountain chain – regions characterized by arid conditions and/or abundant cliffs and caves conducive to fossil deposition and preservation. Conversely, the Great Plains and southeastern North America consistently exhibited the lowest preservation potential. While preservation potential generally declined with increasing latitude during the LGM and DG, regions $> 60^\circ\text{N}$ showed high preservation potential during the HOL.

Ecological niche reconstruction

Real and virtual species niches

Although the ENMs based on real world occurrences were not the primary focus of our study, we describe them here to illustrate the range of environmental niches we aimed to represent with virtual species. The six small mammal species covered the bulk of modern North American environments (Fig. 3, Supporting information). Both *Blarina* spp. had the smallest abiotic niches, favoring high mean annual temperature and annual precipitation environments. *Lepus californicus*, a generalist, occupied a broader abiotic niche that included higher elevations, steeper slopes, and greater precipitation seasonality. *Neotoma albigula* occupied a similar, albeit narrower, niche to *L. californicus*, favoring environments with

lower annual precipitation. *Microtus pennsylvanicus* occupied habitats with strong temperature and precipitation seasonality, high annual precipitation, and steep, high-elevation terrain. In contrast, *S. floridanus* favored warm, wet, low-elevation, and relatively flat habitats. The virtual counterparts of these species occupied analogous environmental niches in the past and partially overlapped with the preservation niche in each time period, indicating they effectively captured the primary effects of the preservation biases on ENMs (Fig. 3, Supporting information).

Niche reconstruction accuracy

For all virtual species, the distance between the true and reconstructed niche centroids was consistently smaller when occurrences were sampled from the unbiased layer than from the preservation-biased layer (Fig. 4, Supporting information), except for two species (*V_B. brevicauda* and *V_L. californicus*) in the HOL at $n=25$ (Supporting information). Centroid distances were typically largest in either the LGM or DG, except for *V_M. pennsylvanicus* (Supporting information). Sample size had minimal impact on centroid distance, except at smaller sample sizes ($n=25$ and $n=50$), where distances were slightly greater (Supporting information). At $n=200$, the 25% KDE band of centroids from the unbiased sample layer consistently overlapped the true centroid (Fig. 4, Supporting information), whereas biased sample centroid KDEs failed to overlap the true centroid KDEs, with more pronounced differences in the DG or LGM (Fig. 4, Supporting information). There was no consistent environmental direction of the bias across, or within, time periods and species (Supporting information), likely due to the PCA being calibrated on the virtual species true niche rather than a background environmental sample.

Distribution prediction accuracy

Using biased samples of species occurrences (i.e. those modified by preservation potential – Box 1) in MaxEnt models generally reduced their predictive accuracy (i.e. increased

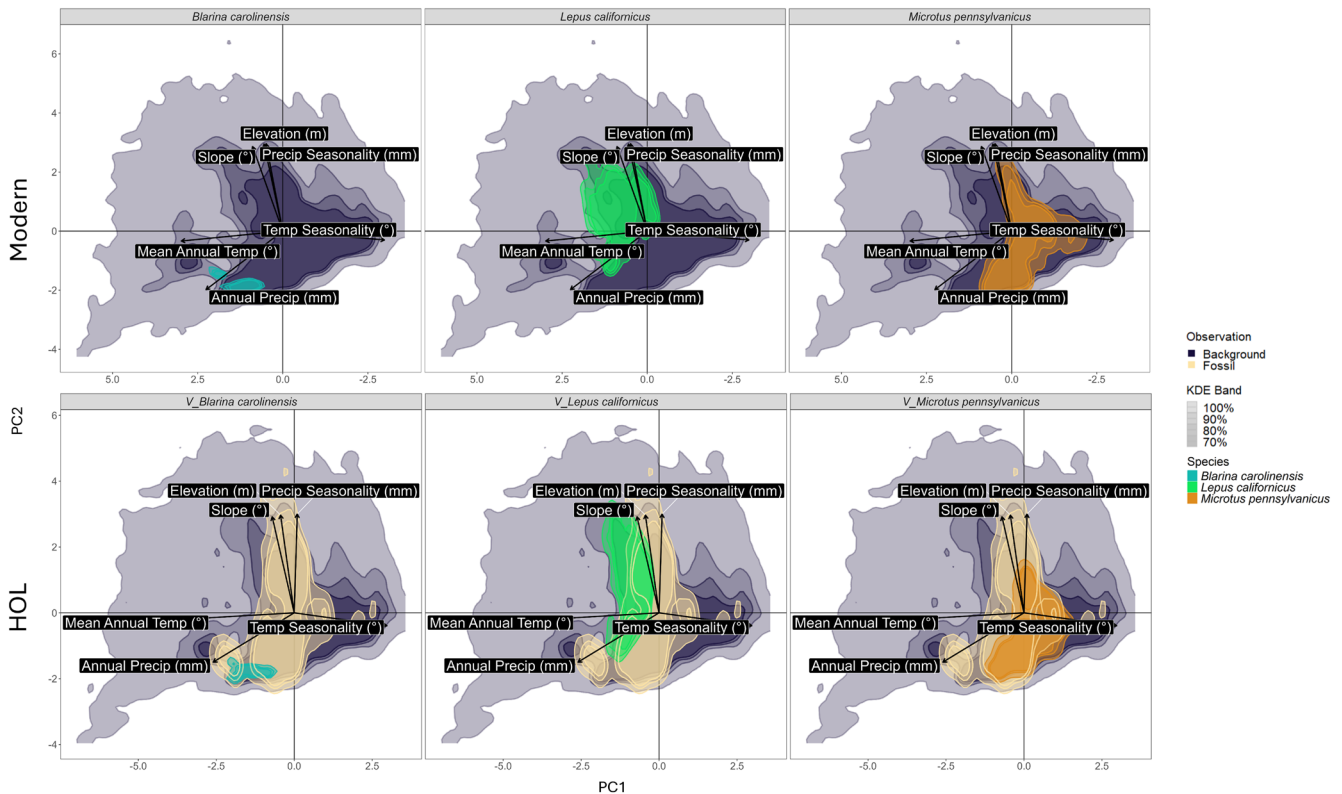


Figure 3. The niche space of three example species (*Blarina carolinensis*, *Lepus californicus*, *Microtus pennsylvanicus*) in the present day (Modern) and the Holocene (HOL) period. Purple polygons represent four kernel density estimates (KDE; 70–100%) bands around the 99 999 samples of North American environments for each time period; pale-yellow polygons show the three KDE (70–90%) bands around the fossil occurrences in HOL. The species niches in the modern are based on the thinned occurrence data of the real species, used to train the ecological niche models, while the species niches in HOL are derived from the ‘true virtual’ species occurrence samples, used as a baseline for comparisons. The x-axis for modern occurrences is reversed to align the orientation of the environmental variables between the two plots. All references to our virtual species are prefixed with V_ followed by the species name.

their median absolute error; MAE), although this effect varied by time period, sample size, and species (Fig. 5A, Supporting information). Specifically, the differences in predictive accuracy between models based on unbiased versus biased samples were typically more pronounced at larger sample sizes and for the LGM or DG. Among the six virtual species, the greatest performance disparities between models trained on unbiased versus biased samples occurred for *V_B. brevicauda*, *V_B. carolinensis*, *V_S. floridanus* and *V_M. pennsylvanicus* in the DG in favor of unbiased samples, although performance differences were minimal ($< 0.25\%$ MAE) for these species in the LGM and HOL (Supporting information). Likewise, *V_L. californicus* and *V_N. albigula* models trained on unbiased samples consistently showed lower average MAE than those trained on biased layers, with the largest performance differences occurring in the LGM and HOL (Fig. 5B, Supporting information). In contrast, *V_B. carolinensis* showed lower average MAE in biased samples in the DG and HOL but not the LGM. Predictive accuracy generally increased with increasing sample size across all time periods (Fig. 5A, Supporting information), though performance gains often diminished or reversed beyond $n=200$ (Fig. 5A, Supporting information).

For $n \geq 200$, the increase in MAE from preservation potential was greatest in species whose niches only partially overlapped with the preservation niche (i.e. the environmental niche of preservation shown in our biplots – Fig. 2A; *V_L. californicus*, *V_M. pennsylvanicus*, *V_N. albigula*), compared to those whose niches predominantly fell within it (*V_Blarina* spp., *V_S. floridanus*) (Fig. 3, 5, Supporting information). Within species, the accuracy differences between models trained on unbiased versus biased samples were greatest in time periods with lower overlap between the species niche and the preservation niche. For instance, *V_M. pennsylvanicus*, which partly occupies environments with strong temperature seasonality (Fig. 3), exhibited the greatest increase in MAE during the DG (Fig. 5B), when the preservation niche overlapped least with strong temperature seasonality (see also *V_B. brevicauda*; Supporting information). Similarly, *V_L. californicus*, whose niche includes high mean annual temperature environments outside the preservation niche (Fig. 3, Supporting information), showed the largest MAE increase in time periods when such environments were most underrepresented (Fig. 5B, Supporting information).

When considering niche reconstruction and predictive accuracy together, the ratio of each sample centroid’s distance

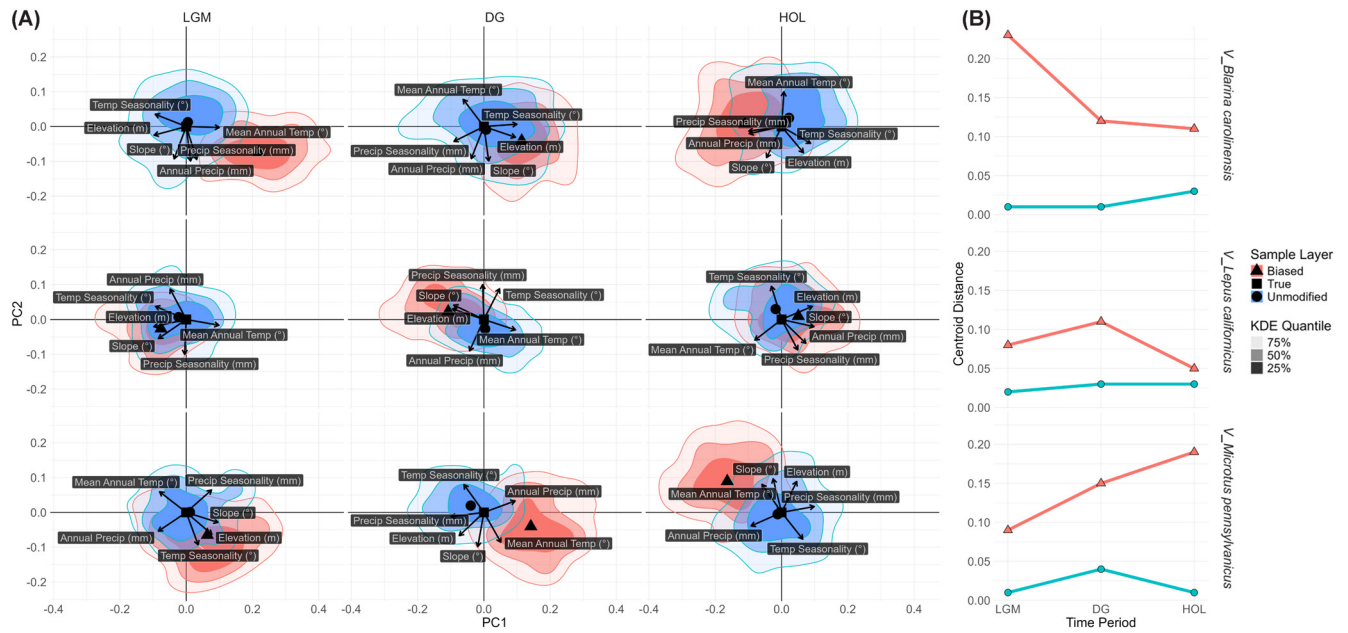


Figure 4. Comparison of species niches derived from sample layers (Unbiased and Biased) relative to 'true' species niches for three virtual species (*V_Blarina carolinensis*, *V_Lepus californicus*, *V_Microtus pennsylvanicus*) for each time period (Last Glacial Maximum [LGM], deglacial [DG], Holocene [HOL]) for $n=200$. (A) Biplots show the distribution and density of 100 replicate centroids for each sample layer (unbiased and biased) relative to the 'true' centroid (square); three kernel density estimate bands are also shown. The circle and triangle indicate the average of the 100 replicate centroids of the unbiased and biased samples, respectively. (B) Shows the average distance of the 100 replicate centroids for the biased and unbiased samples from the true centroid.

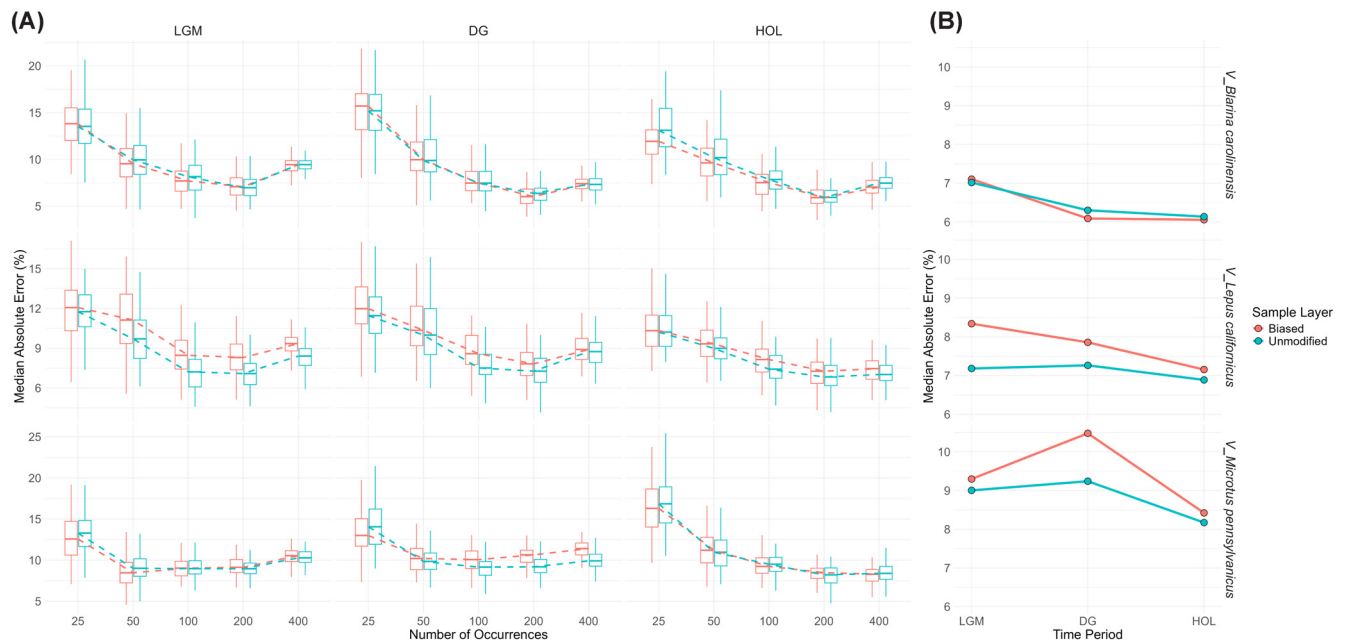


Figure 5. (A) Median absolute error (MAE) of the models for each sampling regime averaged over their 100 replicates. Box plots show the interquartile range, median and outliers for each time period (Last Glacial Maximum [LGM], deglacial [DG], Holocene [HOL]; columns) $\times$ virtual species (*V_Blarina carolinensis*, *V_Lepus californicus*, *V_Microtus pennsylvanicus*; rows) $\times$ sample size (x-axis) and sample layer (unmodified and biased; blue/red respectively). Each plot is overlaid with a trend line of the median value to help visualize the effect of increasing sample size. (B) The average MAE for each sample layer across 100 replicates for the 200-occurrence sample size across the three time periods.

to true centroid (i.e. unbiased centroid distance / biased centroid distance) generally mirrored the trend in MAE for predicted distributions, with the largest ratios observed in time periods that exhibited the greatest differences in MAE (Fig. 4B, 5B).

Discussion

The paleo-record is essential for robust estimates of species' niches and understanding human impacts on ecosystems (Dietl and Flessa 2011, Svenning et al. 2011, Varela et al. 2011, Johnson et al. 2017, Fordham et al. 2020, Raiter and Hawlena 2024), but its utility is constrained by preservation biases (Behrensmeyer and Kidwell 1985, Bellvé et al. 2025). Here we have evaluated how preservation biases manifest across spatiotemporal and environmental gradients and examined their impacts on reconstructing species' ecological niches and geographic distributions. We show that fossil preservation potential varies both spatially and temporally. Spatially, warm and wet environments, as well as those with strong temperature seasonality, exhibit low preservation potential and fall outside the preservation niche. Temporally, the Holocene and deglacial intervals have the highest and lowest mean preservation potential, respectively. Importantly, we demonstrate that variation in preservation potential can distort ecological niche reconstructions, increase prediction error of geographic distributions, and ultimately lead to erroneous ecological inferences. To mitigate these issues, we provide spatially explicit preservation potential layers – particularly useful for modeling late Quaternary distributions of small mammals – and encourage their use to account for preservation bias in paleoecological analyses. For example, the preservation potential layers could be used to correct for preservation biases in ENMs of small mammals during the late Quaternary by weighting background point selection to mimic occurrence sampling biases (Phillips et al. 2009). Our framework provides a novel quantitative advance that can be applied across taxa, time periods, and regions, offering a path forward toward more accurate reconstructions of past distributions and niches, and deeper insights into how environmental conditions influence fossil preservation.

Preservation biases

The low overlap of the preservation niche with warm-wet environments or those with strong temperature seasonality aligns with known patterns in microclimatic fossil preservation (Behrensmeyer and Kidwell 1985) and DNA degradation (Kistler et al. 2017). The paucity of fossils in warm-wet conditions is likely driven by increased microbial activity, which accelerates decomposition (Noto 2011, Behrensmeyer 2021), while strong temperature seasonality drive freeze-thaw cycles that can accelerate bone weathering through cracking (Pokines et al. 2016). Our findings contrast with a recent study on avian fossil formation (Gardner et al. 2016). Few studies, however, examine preservation biases at

the continental scale using approaches similar to ours, and differences between the studies may be due to methodological differences.

Associations between climate and preservation potential were largely consistent across the late Quaternary but differed in strength across specific time periods. The deglacial, while not the warmest, wettest, or most temperature-seasonal period analyzed, exhibited the overall lowest preservation potential, likely due to interactions among climatic factors. For instance, while the highest annual precipitation occurred during the LGM, the deglacial was characterized by generally higher mean annual temperatures and the second-highest annual precipitation levels, conditions that together likely accelerated bone degradation. In contrast, the Holocene, despite being the warmest period, had the lowest annual precipitation, which may have inhibited bone degradation (Munkres 2009). Importantly, differences in the number of fossil sites among the three time periods may have contributed to differences in the preservation potential. Specifically, the LGM had fewer fossil sites, perhaps because fossils have had more time to degrade. As such, preservation potential might be more challenging to estimate in deeper time periods. Still, in our case, the differences in the predictive accuracy of preservation potential models among the three time periods were relatively small, indicating robustness of the models to differences in sample size.

Climate alone does not appear to fully explain the variation in preservation potential during the late Quaternary, nor do we expect it to, given the difficulty of capturing the complexity of fossil preservation using broad-scale environmental variables (Behrensmeyer et al. 2000). The Holocene's high preservation potential is partly due to the abundance of fossil sites from 'Archaeological', i.e. anthropogenic, depositional environments. Though evidence of human occupation in North America exists throughout the late Quaternary (Bennett et al. 2021), 95% of the archaeological fossil sites in our dataset are from the Holocene. As humans expanded across North America, they simultaneously expanded the preservation niche by accumulating, crafting, and caching animal remains (Davis 1987). Our findings demonstrate that the interplay of climate and anthropogenic factors creates a shifting mosaic of preservation across time and space, with consistent patterns emerging at broad spatiotemporal scales.

Reconstructing niches and distributions

Spatial and temporal variability in preservation potential has significant implications for reconstructing species' niches and predicting their geographic distributions. As expected, the effects of preservation bias were greatest when a species' niche fell outside the preservation niche. Species that favor warm-wet habitats or areas with strong temperature seasonality are thus likely to be underrepresented in the fossil record. Such a paucity of records from low-preservation-potential environments may distort modelled niches and distributions if fossil data are naively used to train ENMs (Inman et al. 2018). While we did not, on average, observe larger differences in distribution accuracy between unbiased and biased models

– as we did for niche reconstruction accuracy – we contend that misrepresentations of species niches will still lead to inaccurate distribution predictions across at least part of a species' range, and likely weaken the transferability of the model when predicting to new regions or time periods (i.e. forecasting and hindcasting). Furthermore, it is rarely known a priori which fossil records or locations will produce biased estimates. For this reason, we advocate a conservative approach that accounts for preservation biases whenever possible.

Temporal variation in preservation potential may additionally impact the identification and interpretation of species' niche dynamics. For instance, the increase in preservation potential from the deglacial to Holocene may create the illusion of niche or range expansions, as previously underrepresented environments become better captured in the fossil record. Conversely, changes in preservation potential could obscure actual niche shifts if newly occupied environments coincide with conditions unfavorable for preservation. Such distortions hinder our ability to understand species responses to environmental change and untangle community assembly processes (Behrensmeyer and Kidwell 1985, Fernández-Jalvo et al. 2011, Noto 2011).

As the modern climate changes rapidly, understanding abiotic constraints on species' niches and their responses to past environmental changes is critical for conserving biodiversity. Many species' current niches are truncated by available environmental conditions (Chevalier et al. 2024) and marred by anthropogenic absences (Raiter and Hawlena 2024), suggesting that contemporary occurrences often fail to capture the full abiotic niche of a species. While the fossil record has long been considered a promising avenue for addressing these knowledge gaps, preservation biases have limited its utility. With many regions predicted to experience higher rainfall and temperatures (Trenberth 2011), accurately characterizing the niches of species that occupy such conditions is critical for forecasting their response to contemporary changes (Zhu et al. 2014, Lima-Ribeiro et al. 2017, Nguyen and Leung 2022, Chevalier et al. 2024). Correcting for preservation biases in the fossil record can help accomplish this goal (section 'Conclusions and future directions').

Other regions, taxa, and time periods

Our findings have important implications for paleoecological research beyond the late Quaternary, where studies often span hundreds of thousands of years encompassing substantial climatic and other earth system changes and are characterized by sparser fossil records (Blois et al. 2025). For instance, the Quaternary (the last ~ 2.6 million years) has seen many abrupt climate transitions (Adams et al. 1999), signaling that dramatic shifts in preservation potential have likely occurred, given the variation we observed over just the last 21 000 years. Likewise, preservation potential can be expected to vary across regions with distinct climates, ecological systems, geological and human histories, and among taxa. Megafauna and species with calcified/keratinized components (e.g. Mollusca, Testudinata, etc.) are more likely to leave behind identifiable fossils, while those with pneumatized

bones (e.g. Aves) and/or only soft tissues may be underrepresented (Behrensmeyer et al. 2000, Noto 2011). Extending our framework to deep-time fossil records, diverse regions, and different taxonomic groups could improve ENMs, yielding more accurate reconstructions of past ecological systems and deeper insights into how abiotic factors shape evolutionary trajectories.

Conclusions and future directions

Modern ecological research relies on the fossil record to understand the drivers of biodiversity change over long-time horizons and predict future scenarios. We documented how climatic and anthropogenic controls on fossil preservation potential vary through time and space, leading to mischaracterizations of species' abiotic niches and erroneous predictions of their past distributions. Going forward, we recommend incorporating measures of preservation potential into studies that leverage the fossil record to examine past species niches and distributions. Adjusting for these biases can be achieved by using preservation potential layers, such as ours, to weight background point selection (i.e. the 'FactorBiasOut' method; Phillips et al. 2009; see also Inman et al. 2018, Bellvé et al. 2025, Lee et al. 2025). In habitats where fossils are absent, pooling data from multiple sources (e.g. modern occurrences, historic accounts, etc.) can help generate more accurate models of a taxon's niche (Broennimann and Guisan 2008, Maiorano et al. 2013, Metcalf et al. 2014, Bellvé et al. 2025), though doing so requires careful consideration of each source's biases and contexts, potentially sacrificing spatial or temporal resolution. Ultimately, our proposed approach will enhance our ability to disentangle true ecological patterns from preservation artifacts, improving the reliability of fossil-based inferences.

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Author contributions

André M. Bellvé: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Software (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Val J. P. Syverson:** Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Methodology (supporting);

Writing – original draft (supporting); Writing – review and editing (supporting). **Jessica L. Blois:** Conceptualization (supporting); Data curation (supporting); Funding acquisition (equal); Methodology (supporting); Project administration (equal); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Marta A. Jarzyna:** Conceptualization (equal); Funding acquisition (lead); Methodology (equal); Project administration (lead); Resources (lead); Supervision (lead); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ecog.08085>.

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.mpg4f4rbm> (Bellvé et al. 2025b).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Adams, J., Maslin, M. and Thomas, E. 1999. Sudden climate transitions during the quaternary. – *Prog. Phys. Geogr.* 23: 1–36.
- Aiello-Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B. and Anderson, R. P. 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. – *Ecography* 38: 541–545.
- Baker, D. J., Maclean, I. M. D., Goodall, M. and Gaston, K. J. 2022. Correlations between spatial sampling biases and environmental niches affect species distribution models. – *Global Ecol. Biogeogr.* 31: 1038–1050.
- Barber, R. A., Ball, S. G., Morris, R. K. and Gilbert, F. 2022. Target-group backgrounds prove effective at correcting sampling bias in MaxEnt models. – *Divers. Distrib.* 28: 128–141.
- Barker, J. R. and MacIsaac, H. J. 2022. Species distribution models: administrative boundary centroid occurrences require careful interpretation. – *Ecol. Modell.* 472: 110107.
- Beaumont, L. J., Graham, E., Duursma, D. E., Wilson, P. D., Cabrelli, A., Baumgartner, J. B., Hallgren, W., Esperón-Rodríguez, M., Nipperess, D. A. and Warren, D. L. 2016. Which species distribution models are more (or less) likely to project broad-scale, climate-induced shifts in species ranges? – *Ecol. Modell.* 342: 135–146.
- Behrensmeyer, A. K. 1978. Taphonomic and ecologic information from bone weathering. – *Paleobiology* 4: 150–162.
- Behrensmeyer, A. K. 2021. Taphonomy. – In: Alderton, D. and Elias, S. A. (eds), *Encyclopedia of geology*, 2nd edn. – Academic Press, pp. 12–22.
- Behrensmeyer, A. K. and Hill, A. P. 1988. Fossils in the making: vertebrate taphonomy and paleoecology. – Univ. Chicago Press.
- Behrensmeyer, A. K. and Kidwell, S. M. 1985. Taphonomy's contributions to paleobiology. – *Paleobiology* 11: 105–119.
- Behrensmeyer, A. K., Kidwell, S. and Gastaldo, R. 2000. Taphonomy and paleobiology. – *Paleobiology* 26: 103–147.
- Bellvé, A. M., Wilmshurst, J. M., Wood, J. R., Whitehead, E., Scofield, R. P., Worthy, T. H., Gaskin, C. P. and Perry, G. L. 2025a. Burrowing into the past: extending niche space models of procellariiform breeding grounds by merging fossil and historic data. – *Divers. Distrib.* 31: e70032.
- Bellvé, A. M., Syverson, V. J. P., Blois, J. L. and Jarzyna, M. A. 2025b. Data from: Preservation biases in the fossil record distort species ecological niche and distribution models. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.mpg4f4rbm>.
- Bennett, M. R., Bustos, D., Pigati, J. S., Springer, K. B., Urban, T. M., Holliday, V. T., Reynolds, S. C., Budka, M., Honke, J. S. and Hudson, A. M. 2021. Evidence of humans in North America during the Last Glacial Maximum. – *Science* 373: 1528–1531.
- Block, S., Saltré, F., Rodríguez-Rey, M., Fordham, D. A., Unkel, I. and Bradshaw, C. J. 2016. Where to dig for fossils: combining climate-envelope, taphonomy and discovery models. – *PLoS One* 11: e0151090.
- Blois, J. L., Bellvé, A. M., Jarzyna, M. A., Saupe, E. E. and Syverson, V. J. 2025. Paleobiogeographic insights gained from ecological niche models: progress and continued challenges. – *Paleobiology* 51: 8–28.
- Botella, C., Joly, A., Monestiez, P., Bonnet, P. and Munoz, F. 2020. Bias in presence-only niche models related to sampling effort and species niches: lessons for background point selection. – *PLoS One* 15: e0232078.
- Brodie, J. F. and Mannion, P. D. 2023. The hierarchy of factors predicting the latitudinal diversity gradient. – *Trends Ecol. Evol.* 38: 15–23.
- Broennimann, O. and Guisan, A. 2008. Predicting current and future biological invasions: both native and invaded ranges matter. – *Biol. Lett.* 4: 585–589.
- Castillo, C., Martín-González, E. and Coello, J. 2001. Small vertebrate taphonomy of la Cueva del Llano, a volcanic cave on Fuerteventura (Canary Islands, Spain). Palaeoecological implications. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 166: 277–291.
- Chevalier, M., Broennimann, O. and Guisan, A. 2024. Climate change may reveal currently unavailable parts of species' ecological niches. – *Nat. Ecol. Evol.* 8: 1298–1310.
- Davis, S. J. 1987. The archaeology of animals. – Routledge.
- Dietl, G. P. and Flessa, K. W. 2011. Conservation paleobiology: putting the dead to work. – *Trends Ecol. Evol.* 26: 30–37.
- Elith, J., Kearney, M. and Phillips, S. 2010. The art of modelling range-shifting species. – *Methods Ecol. Evol.* 1: 330–342.
- Faurby, S. and Araújo, M. B. 2018. Anthropogenic range contractions bias species climate change forecasts. – *Nat. Clim. Change* 8: 252–256.
- Faurby, S., Silvestro, D., Werdelin, L. and Antonelli, A. 2024. Reliable biogeography requires fossils: insights from a new species-level phylogeny of extinct and living carnivores. – *Proc. R. Soc. B* 291: 20240473.
- Fernández-Jalvo, Y., Scott, L. and Andrews, P. 2011. Taphonomy in palaeoecological interpretations. – *Quat. Sci. Rev.* 30: 1296–1302.
- Fielding, A. H. and Bell, J. F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. – *Environ. Conserv.* 24: 38–49.
- Foote, M. 2001. Inferring temporal patterns of preservation, origination, and extinction from taxonomic survivorship analysis. – *Paleobiology* 27: 602–630.

- Fordham, D. A., Jackson, S. T., Brown, S. C., Huntley, B., Brook, B. W., Dahl-Jensen, D., Gilbert, M. T. P., Otto-Bliesner, B. L., Svensson, A. and Theodoridis, S. 2020. Using paleo-archives to safeguard biodiversity under climate change. – *Science* 369: eabc5654.
- Fritz, W. J. 1986. Plant taphonomy in areas of explosive volcanism. – Notes for short course: Ser. Geol. 15: 1–9.
- Gardner, E. E., Walker, S. E. and Gardner, L. I. 2016. Palaeoclimate, environmental factors, and bird body size: a multivariable analysis of avian fossil preservation. – *Earth-Sci. Rev.* 162: 177–197.
- Grinnell, J. 1917. The niche-relationships of the California thrasher. – *Auk* 34: 427–433.
- Guisan, A., Thuiller, W. and Zimmermann, N. E. 2017. Habitat suitability and distribution models: with applications in R. – Cambridge Univ. Press.
- Inman, R., Franklin, J., Esque, T. and Nussear, K. 2018. Spatial sampling bias in the Neotoma Paleocological Archives affects species paleo-distribution models. – *Quat. Sci. Rev.* 198: 115–125.
- Inman, R., Franklin, J., Esque, T. and Nussear, K. 2021. Comparing sample bias correction methods for species distribution modeling using virtual species. – *Ecosphere* 12: e03422.
- Johnson, C. N., Balmford, A., Brook, B. W., Buettel, J. C., Galetti, M., Guangchun, L. and Wilmschurst, J. M. 2017. Biodiversity losses and conservation responses in the Anthropocene. – *Science* 356: 270–275.
- Karger, D. N., Nobis, M. P., Normand, S., Graham, C. H. and Zimmermann, N. E. 2023. CHELSA-TraCE21k – high-resolution (1 km) downscaled transient temperature and precipitation data since the Last Glacial Maximum. – *Clim. Past* 19: 439–456.
- Kistler, L., Ware, R., Smith, O., Collins, M. and Allaby, R. G. 2017. A new model for ancient DNA decay based on paleogenomic meta-analysis. – *Nucleic Acids Res.* 45: 6310–6320.
- Kramer-Schadt, S., Niedballa, J., Pilgrim, J. D., Schröder, B., Lindenborn, J., Reinfelder, V., Stillfried, M., Heckmann, I., Scharf, A. K. and Augeri, D. M. 2013. The importance of correcting for sampling bias in MaxEnt species distribution models. – *Divers. Distrib.* 19: 1366–1379.
- Lafuente Diaz, M. A., D'Angelo, J. A., Del Fueyo, G. M. and Zodrow, E. L. 2018. Fossilization model for *Squamastrobis tigrens* foliage in a volcanic-ash deposit: implications for preservation and taphonomy (Podocarpaceae, Lower Cretaceous, Argentina). – *Palaios* 33: 323–337.
- Lee, F., Bellvé, A. M., Alena, H., Asena, Q. and Perry, G. L. 2025. Using population viability analysis and fossil records to inform the conservation of pāteke (*Anas chlorotis*). – *N. Z. J. Ecol.* 49: 1–13.
- Leroy, B., Meynard, C. N., Bellard, C. and Courchamp, F. 2016. virtualspecies, an R package to generate virtual species distributions. – *Ecography* 39: 599–607.
- Lima-Ribeiro, M. S., Moreno, A. K. M., Terribile, L. C., Caten, C. T., Loyola, R., Rangel, T. F. and Diniz-Filho, J. A. F. 2017. Fossil record improves biodiversity risk assessment under future climate change scenarios. – *Divers. Distrib.* 23: 922–933.
- Maguire, E. P., Feldmann, R. M., Casadio, S. and Schweitzer, C. E. 2016. Distal volcanic ash deposition as a cause for mass kills of marine invertebrates during the Miocene in Northern Patagonia, Argentina. – *Palaios* 31: 577–591.
- Maguire, K. C., Nieto-Lugilde, D., Fitzpatrick, M. C., Williams, J. W. and Blois, J. L. 2015. Modeling species and community responses to past, present, and future episodes of climatic and ecological change. – *Annu. Rev. Ecol. Evol. Syst.* 46: 343–368.
- Maiorano, L., Cheddadi, R., Zimmermann, N. E., Pellissier, L., Petitpierre, B., Pottier, J., Laborde, H., Hurdu, B. I., Pearman, P. B., Psomas, A., Singarayer, J. S., Broennimann, O., Vittoz, P., Dubuis, A., Edwards, M. E., Binney, H. A. and Guisan, A. 2013. Building the niche through time: using 13 000 years of data to predict the effects of climate change on three tree species in Europe. – *Global Ecol. Biogeogr.* 22: 302–317.
- Metcalfe, J. L., Prost, S., Nogués-Bravo, D., DeChaine, E. G., Anderson, C., Batra, P., Araújo, M. B., Cooper, A. and Guralnick, R. P. 2014. Integrating multiple lines of evidence into historical biogeography hypothesis testing: a Bison bison case study. – *Proc. R. Soc. B* 281: 20132782.
- Moreno-Amat, E., Rubiales, J. M., Morales-Molino, C. and García-Amorena, I. 2017. Incorporating plant fossil data into species distribution models is not straightforward: pitfalls and possible solutions. – *Quat. Sci. Rev.* 170: 56–68.
- Munkres, J. W. 2009. Arid climate decomposition and decay: a taphonomic study using swine. – MS thesis, University of Nevada, Las Vegas, USA.
- Nguyen, D. and Leung, B. 2022. How well do species distribution models predict occurrences in exotic ranges? – *Global Ecol. Biogeogr.* 31: 1051–1065.
- Nogués-Bravo, D., Rodríguez, J., Hortal, J., Batra, P. and Araújo, M. B. 2008. Climate change, humans, and the extinction of the woolly mammoth. – *PLoS Biol.* 6: e79.
- Noto, C. R. 2011. Hierarchical control of terrestrial vertebrate taphonomy over space and time: discussion of mechanisms and implications for vertebrate paleobiology. – In: Allison, P. A. and Bottjer, D. J. (eds), *Taphonomy: process and bias through time. Aims & scope topics in geobiology book series.* – Springer, pp. 287–336.
- Phillips, S. J., Dudík, M., Elith, J., Graham, C. H., Lehmann, A., Leathwick, J. and Ferrier, S. 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. – *Ecol. Appl.* 19: 181–197.
- Pokines, J. T. and Spiegel, C. 2021. Subaerial weathering and other terrestrial surface taphonomic processes. – In: Pokines, J. T., L'Abbe, E. N. and Symes, S. A. (eds), *Manual of forensic taphonomy*, 2nd edn. – CRC Press, pp. 403–442.
- Pokines, J. T., King, R. E., Graham, D. D., Costello, A. K., Adams, D. M., Pendray, J. M., Rao, K. and Siwek, D. 2016. The effects of experimental freeze-thaw cycles to bone as a component of subaerial weathering. – *J. Archaeol. Sci. Rep.* 6: 594–602.
- Qiao, H., Peterson, A. T., Ji, L. and Hu, J. 2017. Using data from related species to overcome spatial sampling bias and associated limitations in ecological niche modelling. – *Methods Ecol. Evol.* 8: 1804–1812.
- Raite, K. G. and Hawlena, D. 2024. Managing multiple uncertainties in species distribution modelling. – *Divers. Distrib.* 30: e13857.
- Rausell-Moreno, A., Galiana, N., Naimi, B. and Araújo, M. B. 2025. Improving species distribution models by optimising background points: impacts on current and future climate projections. – *Ecol. Modell.* 507: 111177.
- Reimer, P. J. et al. 2020. The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). – *Radiocarbon* 62: 725–757.
- Signor, P. W., III and Lipps, J. H. 1982. Sampling bias, gradual extinction patterns and catastrophes in the fossil record. – In: Silver, L. T. and Schultz, P. H. (eds), *Geological implications of*

- impacts of large asteroids and comets on the earth. Special Paper – Geological Society of America, pp. 190–291.
- Svenning, J.-C., Fløjgaard, C., Marske, K. A., Nógues-Bravo, D. and Normand, S. 2011. Applications of species distribution modeling to paleobiology. – *Quat. Sci. Rev.* 30: 2930–2947.
- Syfert, M. M., Smith, M. J. and Coomes, D. A. 2013. The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. – *PLoS One* 8: e55158.
- Tenorio, E. A., Montoya, P., Norden, N., Rodríguez-Buriticá, S., Salgado-Negret, B. and Gonzalez, M. A. 2023. Mountains exhibit a stronger latitudinal diversity gradient than lowland regions. – *J. Biogeogr.* 50: 1026–1036.
- Thioulouse, J., Dray, S., Dufour, A.-B., Siberchicot, A., Jombart, T., Pavoine, S., Thioulouse, J., Dray, S., Dufour, A.-B. and Siberchicot, A. 2018. The dudi class. – In: *Multivariate analysis of ecological data with ade4*. – Springer, pp. 29–51.
- Tong, R., Yesson, C., Yu, J., Luo, Y. and Zhang, L. 2023. Key factors for species distribution modeling in benthic marine environments. – *Front. Mar. Sci.* 10: 1222382.
- Trenberth, K. E. 2011. Changes in precipitation with climate change. – *Clim. Res.* 47: 123–138.
- Varela, S., Lobo, J. M. and Hortal, J. 2011. Using species distribution models in paleobiogeography: a matter of data, predictors and concepts. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 310: 451–463.
- Vidaña, S. D. and Goring, S. J. 2023. neotoma2: an R package to access data from the Neotoma Paleocology Database. – *J. Open Source Softw.* 8: 5561.
- Williams, J. W., Grimm, E. C., Blois, J. L., Charles, D. F., Davis, E. B., Goring, S. J., Graham, R. W., Smith, A. J., Anderson, M. and Arroyo-Cabrales, J. 2018. The Neotoma Paleocology Database, a multiproxy, international, community-curated data resource. – *Quat. Res.* 89: 156–177.
- Willis, K. J. and Birks, H. J. B. 2006. What is natural? The need for a long-term perspective in biodiversity conservation. – *Science* 314: 1261–1265.
- Wisn, M. S., Hijmans, R., Li, J., Peterson, A. T., Graham, C., Guisan, A. and NCEAS Predicting Species Distributions Working Group 2008. Effects of sample size on the performance of species distribution models. – *Divers. Distrib.* 14: 763–773.
- Zhu, G., Liu, Q. and Gao, Y. 2014. Improving ecological niche model transferability to predict the potential distribution of invasive exotic species. – *Biodivers. Sci.* 22: 223–230.
- Zurell, D., Berger, U., Cabral, J. S., Jeltsch, F., Meynard, C. N., Münkemüller, T., Nehrbass, N., Pagel, J., Reineking, B. and Schröder, B. 2010. The virtual ecologist approach: simulating data and observers. – *Oikos* 119: 622–635.